SOME QUESTIONS OF METHOD IN PHYLLOTAXIS

Irving Adler
North Bennington, VT 05257 USA

Abstract. Past failures to solve the riddle of phyllotaxis were due in part to faulty methods employed in the construction of theories or the assembling of observational data. The following examples of faulty methods are analysed to reveal hidden errors or unwanted consequences: 1) Tait argued that if the numbers of conspicuous left and right spirals are consecutive Fibonacci numbers, then the divergence angle must be between one-third and one-half of a turn. He then concluded that the converse was necessarily true. 2) Schwendener used a force diagram to show that equal and opposite forces were acting at the ends of a line segment AA' in the plane development of a cylindrical surface. He then concluded that the points A and A' were compelled to move apart. 3) Davies and others measured divergence angles on many plants with a given phyllotaxis, and then plotted a frequency distribution of the measured values to show that they cluster about an average value. 4) Richards and others worked exclusively with difficult transcendental equations derived from a disc model of phyllotaxis, although a simple transformation would have converted the transcendental equations into simple algebraic equations. 5) Some investigators overlook the fact that the girth of the stem is a natural unit of length for the study of phyllotaxis. Using other units tends to obscure an important functional relationship that is revealed when the natural unit is used. The analysis of these faulty methods is followed by a discussion of a) the importance of using a phase-space diagram and b) how a mathematical model should be understood.

Keywords. divergence angle; rise; visible opposed parastichy pair; conspicuous opposed parastichy pair; extension.

INTRODUCTION

Phyllotaxis is the study of the arrangement of units such as leaves, florets or scales of a plant around a stem. The arrangement can be represented as a cylindrical point-lattice (a uniform distribution of points on a cylindrical surface) where each point represents the center of a unit. A level on the cylinder (a plane perpendicular to the axis of the cylinder) that contains a lattice point may contain only one or more than one. Since the properties of the case where a level contains more than one lattice point are easily derived from the case where it contains only one, we confine our discussion to the latter. In that case there exists a genetic spiral, a helix on the cylinder that contains all of the lattice points, arranged at equal distances on it like beads on a string, and joining each one to the next by going the shorter way around the stem.

Unit emerges on the genetic spiral at equal intervals of time called plastochrones, and may be numbered consecutively starting with unit 0. If time is measured in plastochrones starting with the emergence of unit 0, then, for any whole number T, unit number T emerges at time T, and for arbitrary T, the number of units present at time T is the greatest integer in T+1.

The divergence angle, d, is defined as the angle of rotation around the axis between successive lattice points, expressed as a fraction of a turn. Then, by definition, $0 < d \leq \frac{1}{2}$. For any given d that is not a unit fraction, there is a unique integer $t > 1$ such that $1/(t+1) < d < 1/t$. Without loss of generality we restrict our attention to the case t=2, since the principal results for this case are easily generalized.

The genetic spiral is usually not conspicuous. What are conspicuous are two sets of secondary spirals, one going up to the left, and the other going up to the right, that join each lattice point with its nearest neighbors. These are known as the conspicuous parastichies. If m and n are the number of left and right conspicuous parastichies respectively, the ordered pair (m,n) is called the phyllotaxis of the stem. Where all the units are on a single genetic spiral, m and n are relatively prime.

The central problem of phyllotaxis is to explain two features of the arrangement of units observed in plants: 1) In nearly all plants with one genetic spiral, as T increases, the divergence angle d rapidly converges toward τ^{-2}, where τ is the golden section ($\tau = (1+\sqrt{5})/2$); and 2) The two numbers m and n in the phyllotaxis of the stem are nearly always consecutive terms of the Fibonacci sequence $(F_n) = 1, 1, 2, 3, 5, 8, 13, \ldots$, where $F_1 = F_2 = 1$, and $F_{n+1} = F_n + F_{n-1}$ for $n > 1$.

The problem has been under investigation since 1830, beginning with papers by Schimper (1830), Braun (1831, 1835) and the Bravais brothers (1837). Never the-less almost 150 years passed before a model of phyllotaxis was developed that provided a rigorously proved explanation of these phenomena (Adler, 1974, 1977). Earlier investigators had some useful intuitions and solved some parts of the problem but never really penetrated to the core of it although they thought they had. They were led astray by faulty methods that included a) failure to define unambiguously the relevant concepts, b) fallacious reasoning, c) a hidden assumption that turns out to be false, and d) selection of parameters and units that

tended to obscure rather than reveal relationships. These were all competent investigators. Nevertheless they stumbled into some common booby traps. An analysis of their errors may be of some use to other model builders as an indication of pitfalls to be avoided. This analysis will be followed by a brief discussion of how a mathematical model should be understood, using the contact pressure model of phyllotaxis as an example.

TAIT'S ERROR

Let us examine first the paper by P.G. Tait (1872) which served as the basis for D'Arcy W. Thompson's chapter on phyllotaxis in his classical work "On Growth and Form." Tait offers the following argument to explain the fact that the number of left and right spirals observed in plants are usually consecutive terms of the Fibonacci sequence. Represent a leaf distribution on a cylindrical stem by a cylindrical point-lattice, and draw the plane development of the cylindrical surface (Fig. 1). Let A and A' represent the same leaf and let O be a leaf that can be reached from A by m steps on a right spiral, and from A' by n steps on a left spiral, with $m > n$. Then there is another common leaf P that can be reached by m-n steps on the right spiral and by n steps on a new left spiral. When m and n are relatively prime, this procedure may be repeated until a leaf is obtained that may be reached in one step on a left or right spiral and by t steps on a right or left spiral respectively. If $t = 2$, the number of leaves in a single turn of the genetic spiral is between 2 and 3, hence the divergence angle is between 1/3 and 1/2. He then concluded that if the divergence angle is between 1/3 and 1/2, "the values of m and n for the most conspicuous spirals must be of the form (2,1), (3,2), (5,3), (8,5), etc."

There are two significant flaws in Tait's argument. 1) He fails to define and distinguish three totally different concepts, only one of which is relevant to his argument. These concepts are: a) an (arbitrary) opposed parastichy pair, b) a visible opposed parastichy pair, and c) a conspicuous opposed parastichy pair. 2) He assumes incorrectly that the procedure of getting lower parastichy numbers by subtraction until he arrives at (2,1) is uniquely reversible to produce higher parastichy numbers from (2,1) by addition.

To expose the first flaw we need the following definitions: Slit the cylindrical surface along the element through lattice point number zero, and unroll it to produce the plane development. Given any two lattice points whose numbers are m and n, we can draw a right spiral On from point O to point n, and a left spiral O'm from point O' to point m. Some of the lattice points appear at equal intervals on On. Others that are not on On lie on right spirals parallel to On, so that there is a minimal set of n right spirals parallel to On that contain all the lattice points. Similarly there is a minimal set of m left spirals parallel to O'm that contain all the lattice points. The m left spirals and n right spirals are called the opposed parastichy pair (m,n). In general, the intersection of one of the m left spirals and one of the n right spirals need not be a lattice point. In the special case where there is a lattice point at every intersection of the m left spirals with the n right spirals, we call the opposed parastichy pair (m,n) visible. (Fig. 2) If points m and n are the nearest neighbors of point O on the right and left respectively, we call the opposed parastichy pair (m,n) conspicuous. It can be proved that conspicuous implies visible. The procedure that Tait was using to produce parastichy pairs with lower numbers is one that I have called contraction. It makes sense only for visible opposed parastichy pairs. In fact it has been proved (Adler, 1974) That if (m,n) is a visible opposed parastichy pair and $m > n$, then the contraction (m-n,n) is also a visible opposed parastichy pair. Similarly, if (n,m) is visible with $m > n$, then so is (n,m-n). When m and n are relatively prime, repeated contraction does indeed lead to either (1,t) or (t,1) as a visible opposed parastichy pair for some integer $t > 1$, and if $t=2$ the divergence angle does lie, as Tait pointed out, between 1/3 and 1/2.

The condition under which a visible opposed parastichy pair may become conspicuous is a separate problem and it depends on another variable, the rise r, defined as the vertical component of the ditance from point O to point 1 on the genetic spiral when the girth of the cylinder is taken as unit of length. We do not go into this problem here.

When Tait said that the condition $1/3 \leq d \leq 1/2$ suffices to produce all parastichy pairs that are consecutive terms of the Fibonacci sequence, he was saying in effect that if m and n are consecutive Fibonacci numbers, then (m,n) or (n,m) is a visible opposed parastichy pair if and only if $1/3 \leq d \leq 1/2$. That this statement is false follows from the fact that a contraction is not uniquely reversible. If (m,n) is a visible opposed parastichy pair, we can substitute the sum m+n for either m or n to produce a new pair whose contraction is (m,n). The parastichy pair (m+n,n) is called the left extension of (m,n), and the parastichy pair (m,m+n) is called its right extension. Moreover, an extension of a visible opposed parastichy pair need not be visible. Suppose a particular opposed parastichy pair (m,n) is visible if and only if d is in the closed interval $[x/y, z/w]$, where x/y and z/w are in lowest terms. The mediant $(x+z)/(y+w)$ between the fractions x/y and z/w lies in the interval between them and hence divides the interval into two segments. It has been proved that the left extension of (m,n) is visible if and only if d lies in the left segment, and the right extension is visible if and only if d lies in the right segment. (Adler, 1974). For example, (2,3) is visible if and only if $1/3 \leq d \leq 1/2$. Then its left extension (5,3) is visible if and only if $1/3 \leq d \leq 2/5$, and its right extension (2,5) is visible if and only if $2/5 \leq d \leq 1/2$. Starting with the visible pair (2,1), the pairs (2,3), (5,3), (5,8), (13,8),...are alternately right and left extensions. Tait failed to specify this fact. Moreover, to guarantee that all the extensions obtained by taking alternately right and left extensions are visible, it is necessary that d be in successively smaller and smaller intervals which in fact constitute a nest of intervals. The only value of d in that nest

is τ^{-2}, contrary to Tait's assertion that any value between 1/3 and 1/2 suffices. Tait's error consisted of two parts: he assumed without justification that the procedure of contraction of a parastichy pair is uniquely reversible, and he assumed that a necessary condition of a valid procedure is a sufficient condition for its reversal. That so important a mathematician as Tait can fall into such elementary errors should serve as a caveat to all model builders.

SCHWENDENER'S ERROR

We consider next the work of Schwendener (1878) who sought an explanation of Fibonacci phyllotaxis in an entirely different direction. He took a step forward from the static diagram employed by Tait by introducing a dynamic model based on the fact that the stem as a whole and its individual leaf primordia are growing. The growing primordia, when they make contact, exert pressure on each other, and he sought to demonstrate that Fibonacci phyllotaxis is the result of this contact pressure. He pictured the leaf distribution as an arrangement of equal circles in the plane development of the surface of a cylindrical stem. Using a diagram much like Tait's, he compared the broken line AOA' to a roof. The contact pressure, he argued, operates like a vertical force pressing down on the roof at O. To determine the consequences of this force, he first resolved it into components in the directions OA and OA'. These forces are transmitted to A and A' respectively. Then he resolved the forces operating at A and A' into vertical and horizontal components (Fig. 3). He obtained in this way a horizontal force at A pointed left, and an equal horizontal force at A' directed to the right. He then concluded that these forces push A and A' apart, compelling the distance between A and A' to grow, at the same time that the vertical force on O pushes O down toward AA'. He used two separate methods to examine the consequences of these conclusions: a) a series of ruler and compass constructions, and b) a simulation of the compression of the gable by a mechanical device with rigid hinged bars to represent the gable, and rigid movable discs to represent the leaf primordia. His final conclusion was that the phyllotaxis was compelled by contact pressure to rise to higher and higher numbers to (5,3), (5,8),(13,8), etc; that this rise in phyllotaxis was accompanied by an oscillation of the divergence angle with diminishing amplitude in successive swings, and convergence to $137\frac{1}{2}^{0}$ (the degree equivalent of τ^{-2}.) He also measured the extreme values of each separate swing. The foundation of his argument was the statement that A and A' are pushed apart by horizontal forces of equal magnitude and opposite directions. Unfortunately the reasoning that led to this statement is fallacious. He overlooked in his argument that A and A' are one and the same point. Two forces with equal magnitudes and opposite directions acting at the same point add up to zero, and a zero force produces no movement. Thus his conclusion that AA' grows in length remains unproved. Nevertheless, his final conclusions that the phyllotaxis rises to (5,3), (5,8), etc and that the divergence angle converges to $137\frac{1}{2}^{0}$ by a sequence of oscillations of diminishing amplitude turns out to be correct if contact pressure begins early. He even had correct measures for the extreme values of each swing in the oscillations. How was it possible to get these correct results on the basis of a fallacious argument? The answer is that, since the growth of AA' was not proved by his argument, its role in the rest of the argument was that of an assumption. The assumed growth of AA' combined with the assumed decrease of the height of O above AA' implied a decreasing rise. His picture of close-packing of equal circles was tantamount to assuming that each primordium was equidistant from its nearest neighbors. Thus he was assuming the conditions that do indeed lead to the consequences he obtained, as demonstrated in Adler (1974,1977). But because his foundation argument was fallacious, his conclusion remained unproved. Moreover, by assuming that contact pressure was always in effect, he was unable to discover that his conclusions need not apply if contact pressure begins late. He made it seem as though there can be no exceptions to Fibonacci phyllotaxis. However, exceptions such as (2,5) and (5,7) phyllotaxis are well known.

Some further analysis of the reason for Schwendener's errors may be helpful. Schwendener was correct in postulating the existence of contact pressure. Where he went astray is in mechanically carrying over into the phyllotaxis problem the force diagrams used in physics and then not using them logically. Instead of transplanting into biology a diagram borrowed from physics, he should have asked himself, "In what way that is intrinsic to a biological system does contact pressure manifest itself?" The clue to the answer to this question is present in the remark by Schimper (1830) that the leaf primordia, while tending to grow apart, are at the same time constrained to grow toward each other. This clue became the basis of the contact pressure postulate in Adler (1974) that contact pressure expresses itself in the maximization of the minimum distance between primordia. On the basis of this assumption, and the assumption that the rise r is a decreasing function of time, it was possible to prove that Fibonacci phyllotaxis continues under contact pressure if and only if it is already present when contact pressure begins, and that Fibonacci phyllotaxis is inevitable if contact pressure begins early. If it does not begin early, other types of phyllotaxis like (2,5) and (5,7) are also possible. The general lesson to be learned from Schwendener's errors are these: 1) The use of an analogy from another discipline can be helpful, provided that the parameters appropriate to that discipline are not arbitrarily imposed on the subject at hand, where they may be inappropriate. In applying the analogy, it is necessary to find and use those parameters that are intrinsic to the problem under investigation. 2) A general conclusion that leaves no room for exceptions that do occur cannot be valid. The argument that led to the conclusion should then be re-examined to see if some other assumption not explicitly stated had been unconsciously used to arrive at the conclusion. Formulating this assumption explicitly may reveal that it is not always valid. Then it will be clear that the conclusion follows when it is valid, and the exceptions may occur when it is not. In this instance the assumption tacitly made

by Schwendener was that contact pressure begins immediately.

WHEN NOT TO AVERAGE

The two examples discussed so far concerned errors in reasoning made by people trying to construct a theory of phyllotaxis. The next example deals with a methodological flaw that sometimes occurs in the organization of observational data. Many experimentalists (for example, Davies, 1939), after measuring the divergence angle on different regions of a stem or on different stems then proceed to plot a frequency distribution to show that the average divergence angle is very nearly the Fibonacci angle of $137\frac{1}{2}^{\circ}$. This procedure would make sense if there were grounds to believe that the divergence angle is essentially a constant, and that the deviations from the expected value are random fluctuations due to extraneous causes. Then averaging the measures could eliminate the random fluctuations and reveal the constant around which they fluctuate. However, as shown in the contact pressure model of Adler (1974), the divergence angle for any given phyllotaxis (m,n) is not a constant, but is a function of the rise r. In fact, the point (d,r) in the (d,r) plane lies on a circle whose equation expresses the fact that leaves m and n are equidistant from leaf 0. Averaging the measured divergence angles, instead of revealing this dependence of d on r, effectively hides it. The lesson to be learned from this error is that when variations are found in some parameter being measured whose values tend to cluster around a central value, it is not necessarily appropriate to average the measures to eliminate the variations. The variations may be due to an intrinsic functional relationship rather than random deviations.

CHOICE OF UNITS

The subject of my next example is the choice of units of measure. It may seem that choosing a unit of measure is a purely arbitrary matter, and that it makes no difference whether you choose one unit or another. There are circumstances, however, where an arbitrary choice need not and should not be made because a natural unit of measure exists. For example, in the measurement of angles in the calculus, the natural unit of measure is the radian, and using this unit simplifies considerably the power series expansions for the trigonometric functions. In spherical geometry there is a natural unit of length, the circumference of a great circle. Similarly, in phyllotaxis there is a natural unit of length. The phenomenon of phyllotaxis occurs in the same form in plants of various sizes. Therefore the size of the plant is not relevant to its phyllotaxis. What is relevant is the relationship of parts of the plant to the whole. For this reason, a natural choice for the unit of length is the girth of the stem. With this choice of unit, all plants of different sizes are reduced to one normal form, and the extraneous factor of absolute size is eliminated. One of the consequences of using a natural unit is that it may help to reveal relationships that may be obscured by a different choice of unit. For example, Adler (1974), using the girth of the stem as unit of length, showed that, for any given phyllotaxis under conditions of contact pressure, the divergence angle is a linear function of the square of the minimum distance between primordia. Choice of a different unit of length obscures this relationship and may make it well nigh impossible to discover it.

CHOICE OF SURFACE

During the 150-year period in which the phenomena of phyllotaxis have been studied, several different surfaces have been used to model their occurrence. The earliest investigators (Schimper, Braun, Bravais, etc), studying a mature stem, used a cylindrical surface as a close approximation of the surface of the stem. Later investigators (Church, Snow, Richards, etc) argued that the origin of phyllotaxis should be sought on the growing tip of the stem on which leaf primordia first emerge, and not on the elongated mature stem. They therefore rejected the cylindrical picture and turned to the essentially parabolic growing tip. Since they studied the tip by examining cross-sections perpendicular to the axis of the stem, they replaced the cylindrical picture of phyllotaxis by a disc picture (the so-called "centric" representation) in which the conspicuous parastichies have the appearance of logarithmic spirals. A simple transformation can convert the disc picture into a cylindrical picture in which the logarithmic spirals become helices, and the plane development of the cylindrical picture converts every helix into a straight line. Completely overlooking these possibilities, the third generation of students of phyllotaxis worked only with the disc picture. As a result, they became entangled in complicated transcendental equations where simple algebraic equations suffice to express the same relationships in the cylindrical representation. There can be no doubt that the difficulty of working with the transcendental equations of the centric representation stood in the way of penetrating to the core of the problem of phyllotaxis. The return by Adler (1974) to the cylindrical representation and its simpler equations made it easier to move toward a solution of the problem.

A legitimate question can be raised about the cylindrical representation normalized by taking the girth of the cylinder as unit of length, and picturing a leaf distribution as a cylindrical point-lattice. Doesn't this oversimplify a leaf distribution so much that it becomes a falsification? My answer to this question is that the simplification is essential to the study of the problem. Each leaf primordium is actually a three-dimensional appendage on the stem. Different primordia and different parts of one primordium grow at different rates. Neighboring primordia are in contact all along their surfaces. (See the excellent drawings of Williams, 1974.) Nevertheless, as argued in Adler (1977), the contact pressure relations of these three-dimensional appendages may be pictured as relations among points in a cylindrical surface, just as the projective relations of the lines in a bundle of lines through a point may be pictured as relations among points in a projective plane. Picturing the growth of the primordia as a movement of separation of the points that represent them may be thought

of as a kind of integration without benefit of the calculus, attaching to each point the summation of the movements of the different parts of the primordium it represents. Perhaps someone some day, with appropriate assumptions about the shape of primordia and the varying growth rates of their different parts will do such an actual integration on a computer. Meanwhile the normalized cylindrical representation seems to be a reasonable shortcut, and it has justified itself by producing results.

THE PHASE SPACE

Actually even the cylindrical representation of phyllotaxis does not give the best picture of the essential relationships involved. The essence of the problem begins to become clear only in the phase space, the (d,r) plane. There the question to be answered is, "With the passage of time, what is the path followed by the point (d,r) that represents the state of the system?" The answer supplied by the contact pressure model is that the (d,r) plane contains many zig-zag paths, and the lower the value of r, the more paths there are side by side. (Fig. 4). When contact pressure begins, the point (d,r) moves to the nearest such path and then, as long as the rise r decreases and contact pressure continues, it descends along this zig-zag path. Each path is made up of arcs of circles very precisely defined. The diminishing length of the arcs is responsible for the convergence of the divergence angle d to a limit. In the case of the path that begins with the arc along which leaves 1 and 2 are the nearest neighbors of leaf 0, the convergence is to γ^{-1}, the golden angle. The full explanation of the phenomena of phyllotaxis thus becomes clear in the phase space rather than in any of the surfaces in which the phenomena are observed. It seems to me that there is a clear lesson here for model builders: When you look for relationships among observational data, and for a causal explanation of these relationships, don't limit yourself to surface appearances. Look beneath the surface for underlying relationships and trends. Sometimes a seemingly abstract picture may reveal more than the physical picture that is immediately presented to the eye, because the abstract picture may cut away all the extraneous factors present in the physical picture and focus attention on the kernel of the problem. In particular, the abstract phase space should not be neglected as a source of information and insight.

THE MEANING OF A MODEL

I turn now to some brief comments on how a mathematical model in general, and the contact pressure model of phyllotaxis in particular, should be understood. A mathematical model consists of a set of assumptions and conclusions deduced from these assumptions. The essential meaning of the model is the connection it establishes between the assumptions and the conclusions. The model does not assert that the assumptions are always and everywhere valid in the field under study. Its assertion is a conditional statement that where and when the assumptions hold then the conclusions deduced from them should also hold. In the Adler contact pressure model of phyllotaxis, it is assumed that the rise r is a decreasing function of time, and that, beginning with some time T_c, the minimum distance between primordia in the normalized cylindrical representation is maximized. It is then proved that under these assumptions the phyllotaxis undergoes a series of qualitative changes at appropriate times to higher and higher phyllotaxis, with the changes governed by the addition rule that generates the Fibonacci sequence. This is not an assertion that the rise must decrease or that the minimum distance between primordia must be maximized. What is asserted is that where the two assumptions are valid, and as long as they remain valid, the phyllotaxis will rise in accordance with the addition rule. If, for example, the rise begins to increase, and the primordia are pulled apart as the stem is elongated, then the phyllotaxis is no longer constrained to rise.

A PHYLLOTAXIS WAVE

In my summary of the contact pressure model (Adler, 1977, Vol. 65) I used the "vortex" metaphor to describe the zig-zag path that is followed in the (d,r) plane by the point that represents the state of the system. There are many such vortices in the (d,r) plane, their number increasing as r decreases. When contact pressure begins, the point (d,r) moves into a vortex and descends in it while contact pressure lasts. There is another metaphor, viz that of a wave, that is suggested by the shape of the vortex and by the equations for the plastochrone ratio R in a parabolic and disc model. Let $R_i(T)$ be the plastochrone ratio at time T between leaf i and leaf i-1. Then it is shown in Adler (1977, vol. 65) that in both the parabolic model and the disc model $R_{i+1}(T) = R_i(T-i)$. The zig-zag form of the vortex suggests a wave with diminishing amplitude. The equation just cited implies that the wave is moving, for the following reason. The phase space diagram has a two-fold meaning. The same diagram that represents the state of the system in the (d,r) plane can also be understood to represent the movements of leaf 1 relative to leaf 0 in the plane development of the normalized cylindrical representation. The equation given above implies that the wave governing the oscillatory changes in the divergence angle between leaves 0 and 1 moves upwards to the younger pairs of leaves with the passage of time. This implication of the presence of a wave moving up the stem and governing the oscillation of the divergence angles d_i between pairs of primordia has been largely overlooked. The prediction that such a wave exists should be checked by observations of plant growth. Perhaps the appropriate method to use would be time lapse photography of the growth of a plant stem. Probably the best plant to use would be a sunflower head, because it is so large, the consecutive florets on the genetic spiral are easily identified, and the divergence angles between them can be measured.

REFERENCES

ADLER, I. (1974). J. theor. Biol. 45, 1.
ADLER, I. (1977). J. theor. Biol. 65, 29.
ADLER, I. (1977). J. theor. Biol. 67, 447.
BRAUN, A. (1831). Nova Acta Acad. Caesar Leop. Carol. 15, 197.
BRAVAIS, L.&A. (1837). Annls Sci. nat. Botanique (2) 7, 42; 8, 11.
CHURCH, A.H. (1929). On the Interpretation

of Phenomena of Phyllotaxis. Oxford University Press.
DAVIES, P.A. (1939). Am. J. Bot. 26, 67.
RICHARDS, F.J. (1948). Symp. Soc. exp. Biol. 2, 217.
SCHIMPER, K.F. (1830). Geiger Mag. für Pharm. 29, 1.
SCHWENDENER, S. (1878). Mechanische Theorie der Blattstellungen. Leipzig. Engelmann.
SNOW, M.&R. (1962). Phil. Trans. R. Soc. B. 244, 483.
TAIT, P.G. (1872). Proc. R. Soc. Edinb. 7, 391.
THOMPSON, D.W. (1942). On Growth and Form. Vol. 2, p. 912. 2nd edn. reprinted 1968. Cambridge University Press.
WILLIAMS, R.F. (1975). The Shoot Apex and Leaf Growth. Cambridge University Press.

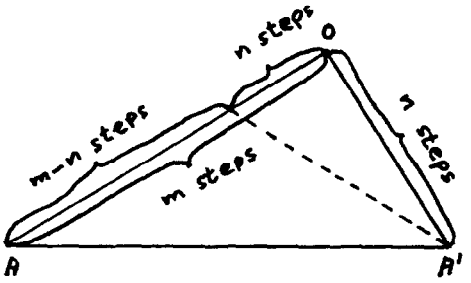

Fig. 1. Tait's contraction of (m,n).

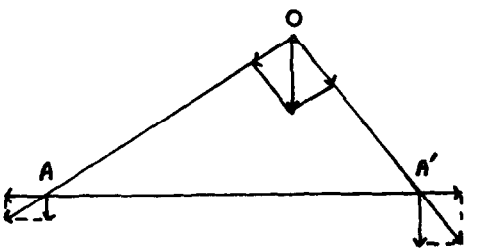

Fig. 3. Schwendener's force diagram.

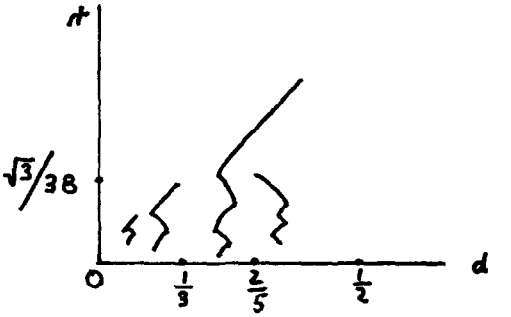

Fig. 4. Schematic diagram of the first few vortices in the (d,r) plane.

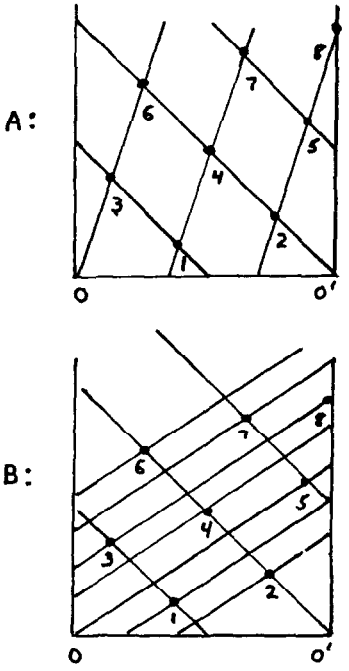

Fig. 2. d=3/8.
A shows (2,3) is visible.
B shows (2,5) is not visible.